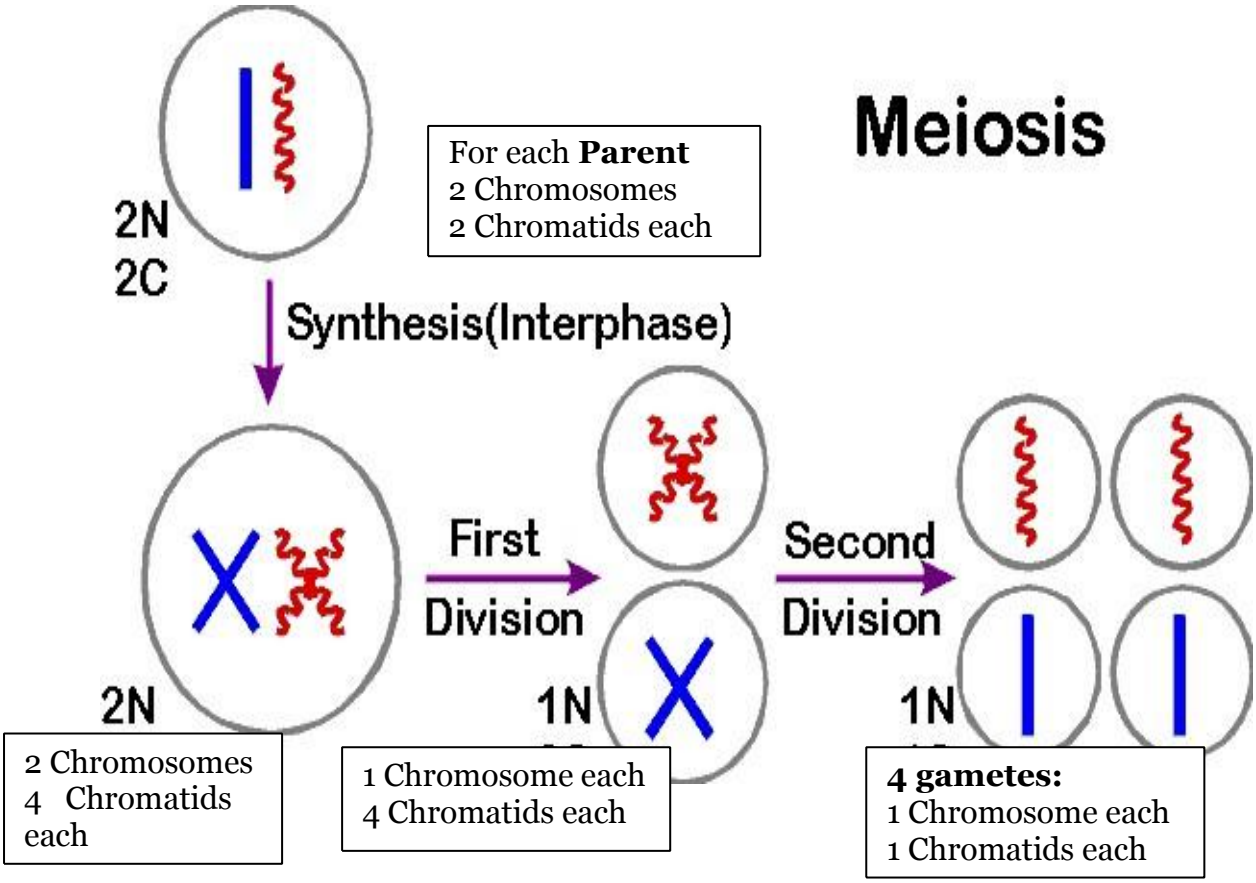
Revise Meiosis process and the relation between Mendel laws and Meiosis before proceeding with this lecture.

Meiosis Action:



LINKAGE AND CHROMOSOME MAPPING IN EUKARYOTES

I. LINKAGE

Genetic linkage is the tendency of genes that are located proximal to each other on a chromosome to be inherited together during meiosis. Genes whose loci are nearer to each other are less likely to be separated onto different chromatids during chromosomal crossover, and are therefore said to be genetically *linked*.

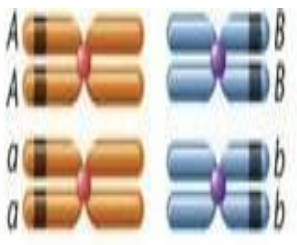
Linked genes: Genes that are inherited together with other gene(s) in form of single unit as they are located on the same chromosome. For example: in fruit flies the genes for eye color and the genes for wing length are on the same chromosome, thus are inherited together.

A couple of genes on chromosomes may be present either on the <u>different</u> **or** on the <u>same</u> chromosome.

1. The independent assortment of two genes located on different chromosomes.

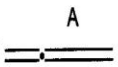
Mendel's Law of Independent Assortment: during gamete formation, segregation of one gene pair is independent of other gene pairs because the traits he studied were determined by genes on different chromosomes.

Consider two genes A and B, each with two alleles A a and B b on separate (different) chromosomes.



Gametes of non-homologous chromosomes assort independently at anaphase producing 4 different genotypes AB, ab, Ab and aB with a genotypic ratio 1:1:1:1. So, when genes are on different chromosomes, **50%** of the gametes produced by a doubly-heterozygous individual are **recombinant**, when compared to the gametes produced by its parents (50% are **parental)**.

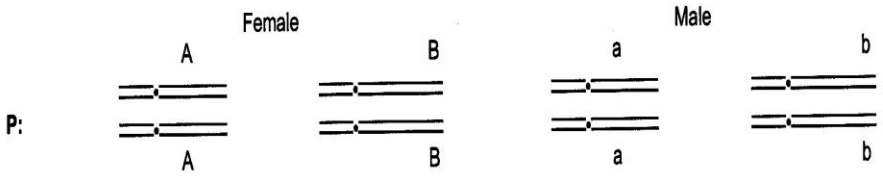
First, consider two genes, each with two alleles A a and B b on separate chromosomes

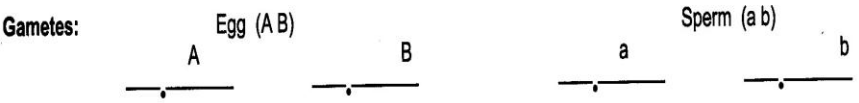
NEW NOTATION: 

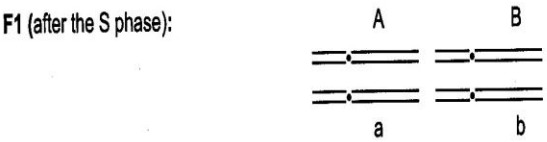
represents the two chromatids of a metaphase chromosome, bearing allele *A* of the *a* locus. 

represents the same chromosome in the single-chromatid stage.

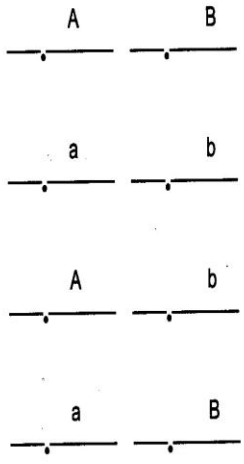
So the cross AA BB x aa bb could be represented as:



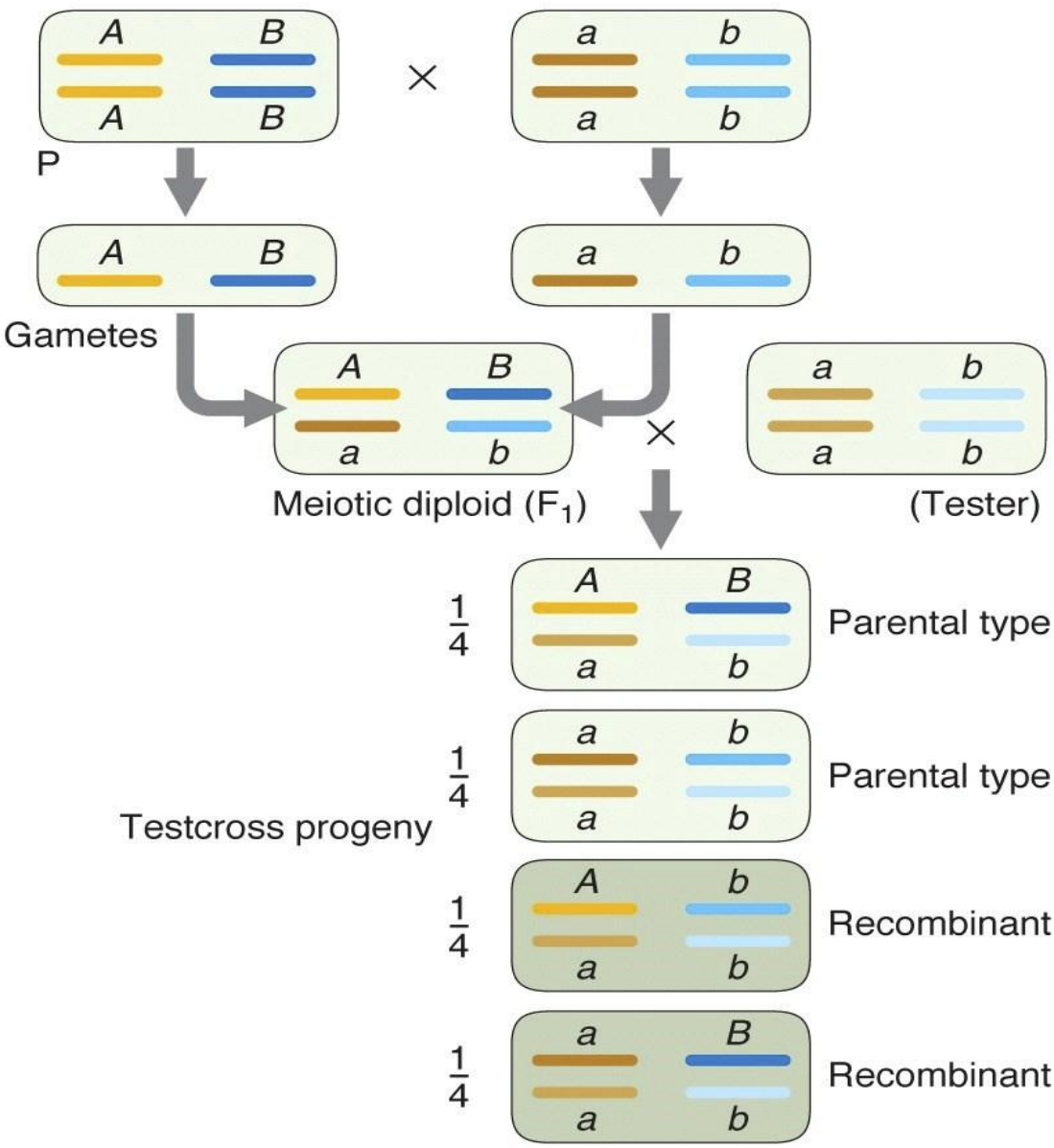




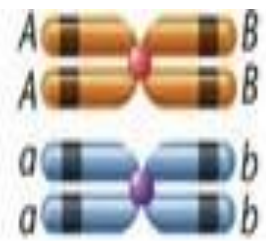
Gametes (non-homologous chromosomes assort independently at anaphase):



	Gamete Genotype	Expected Proportion
Parental	A B	1/4
Parental	a b	1/4
Recombinant	A b	1/4
Recombinant	a B	1/4



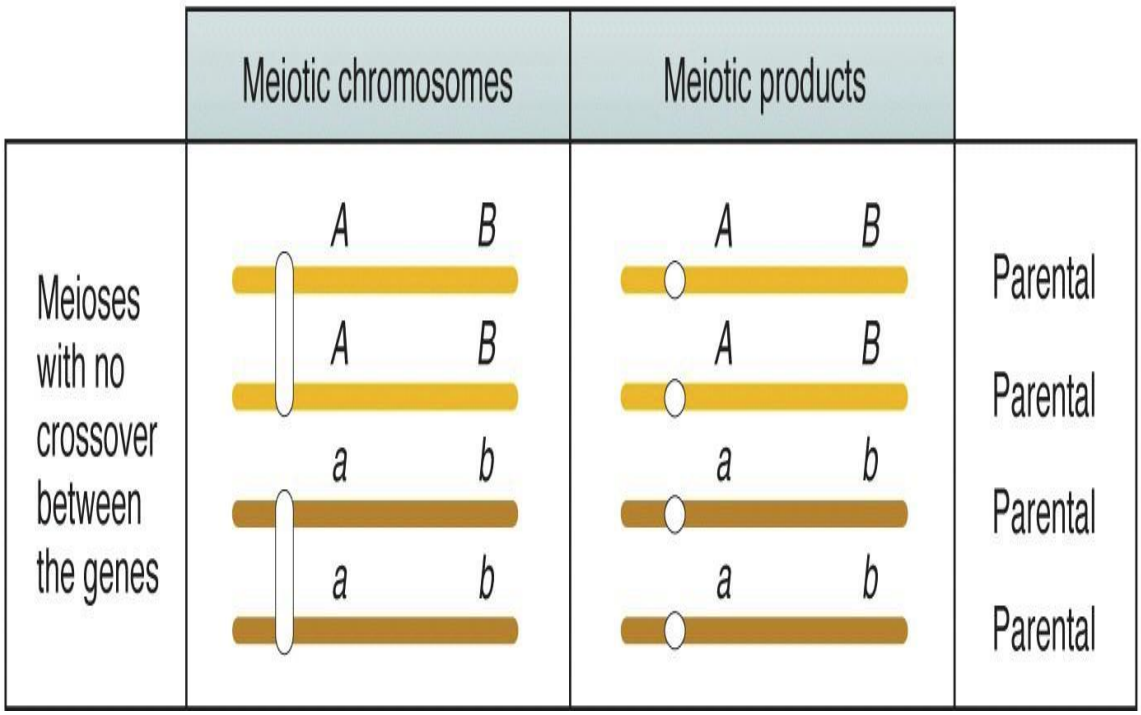
2. If two genes occur on the same chromosome: they may not assort independently at anaphase of meiosis. These genes are said to be LINKED and demonstrate linkage in genetic crosses.



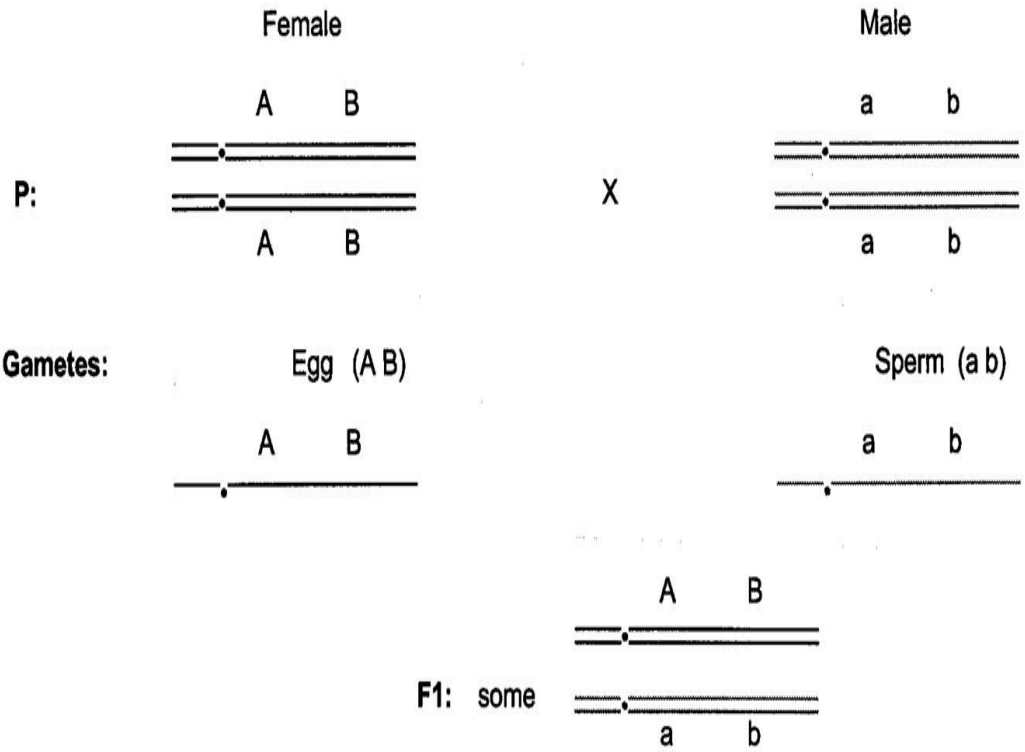
- The two genes are on the same chromosome

(NO CROSSOVER)

If there were no **crossing over**, all the alleles on a single chromosome would segregate together and would end up in the same gamete. This means that **A and B are linked.** With no crossing over, we get only **parental** alleles on the same chromosomes, these results in **100% parental gametes**.



Now consider a case where the two genes are on the same chromosome: (A and B are **linked**)



Gametes resulting from no crossover:

		Expected Prob.
A B	**Parental**	1/4
A B	**Parental**	1/4
a b	**Parental**	1/4
a b	**Parental**	1/4

After Meiosis I and II:

NO CROSSOVER

100% PARENTAL

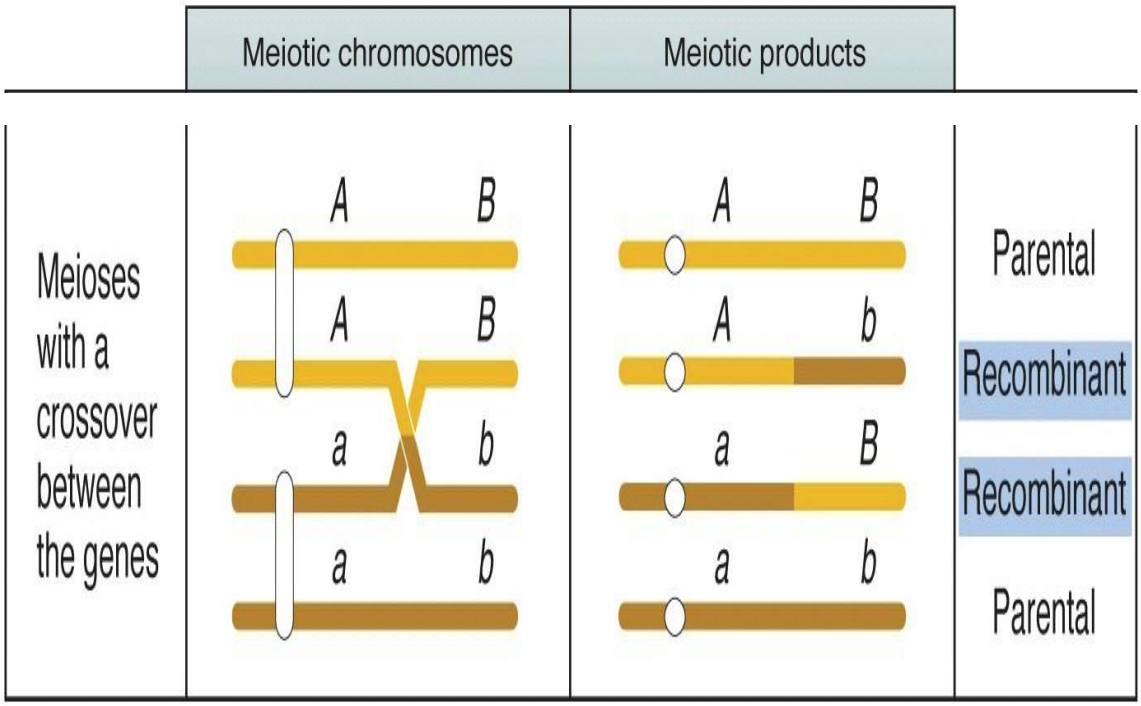
- The two genes are on the same chromosome
  (WITH CROSSING OVER)

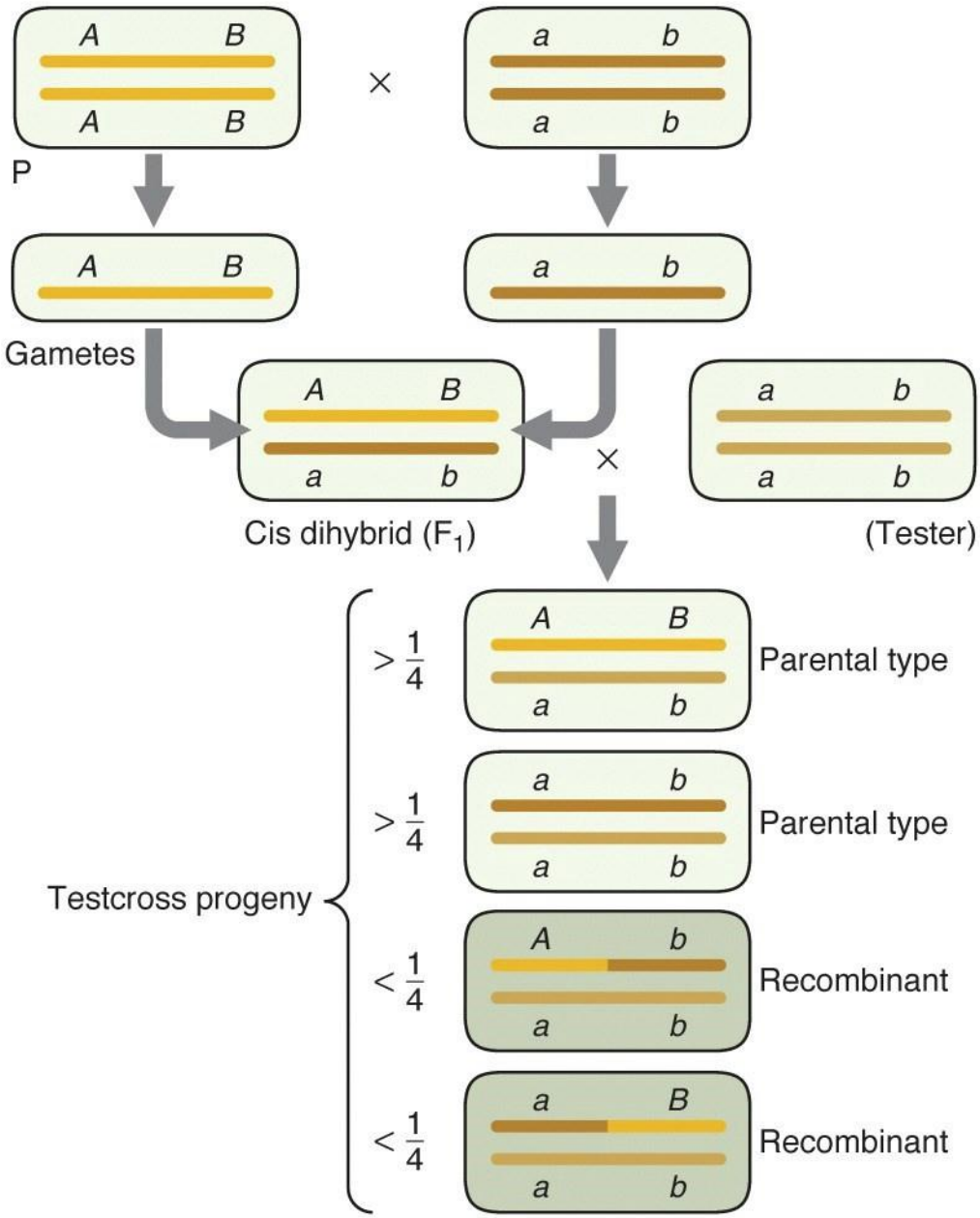
With crossing over, we get **recombination** of alleles on the same chromosomes. Since crossover occurs in the 4-strand stage of meiosis, and involves only two of the four chromatids, each crossover event results in **50% recombinant gametes, and 50% parental gametes**.

So,

Genes on different chromosomes = 50% recombinant gametes after meiosis

Genes on the same chromosome ≤ 50% recombinant gametes after meiosis



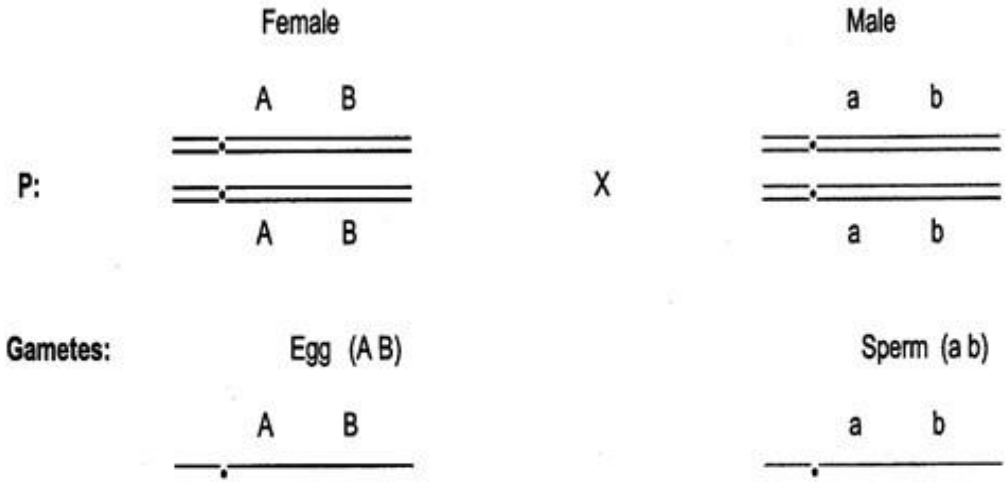


NOTE:

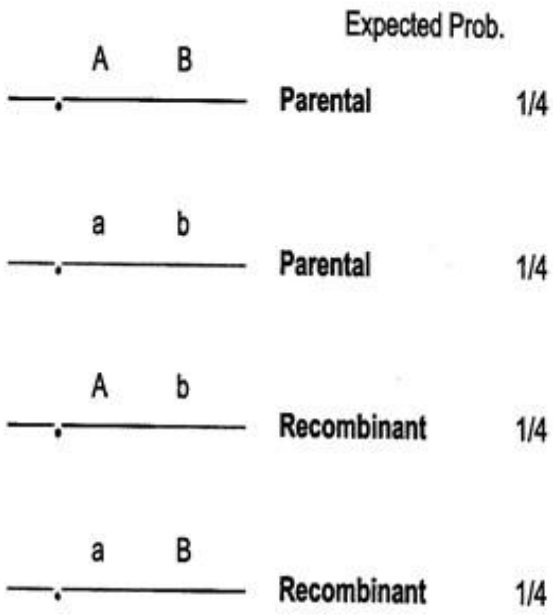
- Each Reproductive Cell (2n) produces 4 gametes (n) at the end of Meiosis II. Crossing Over between 2 non-sister chromatids produces new genetic combinations in half of the gametes, while the other half remain with parental combinations.

- Linked genes present on the same chromosome assorted together into gametes and **Do Not Obey Mendel's Law of Independent Assortment**.

Now consider a case where the two genes are on the same chromosome: (A and B are **linked**)

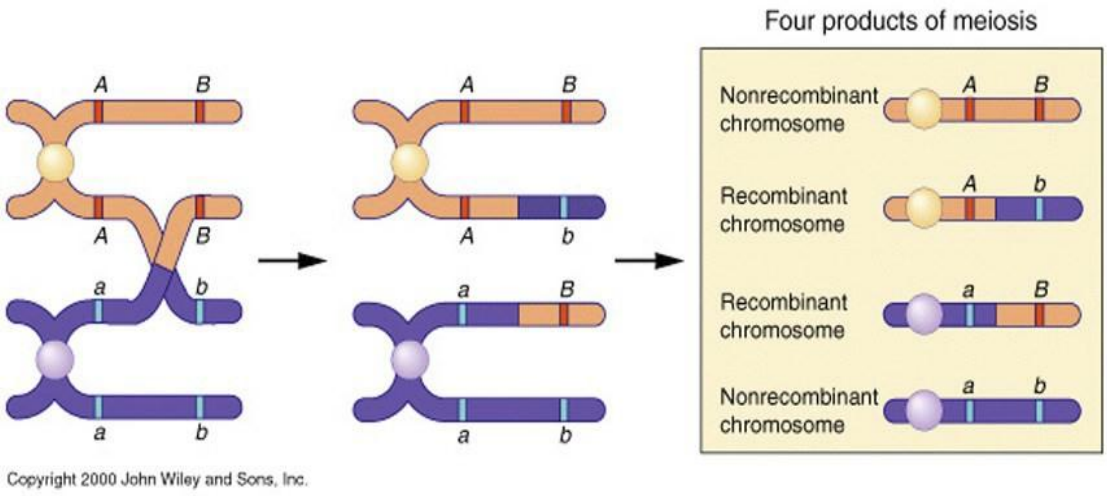


Gametes resulting from crossover:



After Meiosis I and II:

50% recombinant gametes and 50% parental gametes



How Linked genes and Mapping were discovered?

Although Gregor Mendel developed his principles of inheritance in the mid-1800s, the importance of his work went largely unnoticed by the scientific community until the early 1900s.

At that time, numerous researchers began to conduct experiments that upheld many of Mendel's ideas; however, they also discovered several situations that represented apparent deviations from these principles.

Bateson, Saunders and Punnett……Mendel's Exceptions

One of the earliest exceptions to normal Mendelian ratios was observed by the work of geneticists William Bateson, Edith Rebecca Saunders, and Reginald C. Punnett in 1905 with pea plants, these researchers noticed that not all of their crosses yielded results that reflected the principle of independent assortment--specifically, some phenotypes appeared far more frequently than traditional Mendelian genetics would predict. Based on these findings, the trio proposed that certain alleles must somehow be coupled with one another, although they weren't sure how this linkage occurred.

Bateson, Saunders, and Punnett Suspect Linkage

In 1905, William Bateson, Edith Rebecca Saunders, and Reginald Punnett were examining flower color and pollen shape in sweet pea plants by performing dihybrid crosses similar to those carried out by Gregor Mendel. In particular, these researchers crossed homozygous pea plants that had purple flowers and long pollen grains with homozygous plants that had red flowers and round pollen grains. Prior to the cross, the trio noted that purple flowers (P) were dominant over red flowers (p), and that long pollen grains (L) were dominant over round pollen grains (l).

Performing the 1st trial, the F_1 generation of plants resulting from the PPLL x ppll cross was therefore doubly heterozygous (PpLl), and all of the F_1 plants had purple flowers and long pollen grains. Next, Bateson, Saunders, and Punnett decided to cross the F_1 plants with each other. After this cross, the researchers expected the F_2 generation to have a 9:3:3:1 ratio (nine plants with purple flowers and long pollen grains, to three plants with purple flowers and round pollen grains, to three plants with red flowers and long pollen grains, to one plant with red flowers and round pollen grains). Instead, they observed the results shown in the table 1 (below).

Table 1: Characteristics of the F_2 Generation (1st trial)

Phenotype	Expected	Observed	
Purple, long	1199	1528	parental
Purple, round	400	106	recombinants
Red, long	400	117	
Red, round	133	381	parental
Total	2132	2132	

As Table indicates, Bateson, Saunders, and Punnett observed that their crosses produced a deviation from the predicted Mendelian independent assortment ratios. During their analysis, the researchers realized that there was an excess in the number of parental phenotypes (purple-long and red-round) in the F_2 results. In particular, of the 2,132 F_2 plants, 1,199 were expected to have purple flowers and long pollen grains, but instead, there were a whopping 1,528 plants with this phenotype. Similarly, only 133 plants were expected to have red flowers and round pollen grains, but the researchers observed nearly three times that many (381). So, they performed other trials with unchanged deviated ratios (284:21:21:55), figure below. It is now understood that the differences between the expected and observed results were statistically significant ($P < 0.005$), which means that the data could not be explained solely by chance.

Because the parental phenotypes reappeared more frequently than expected, the three researchers hypothesized that there was a coupling, or connection, between the parental alleles for flower color and pollen grain shape and that this coupling resulted in the observed deviation from independent assortment. Indeed, Figure below shows an example of a cross between homozygous pea plants with purple flowers and long pollen grains and homozygous plants with red flowers and round pollen grains that exhibits linkage of the parental alleles.

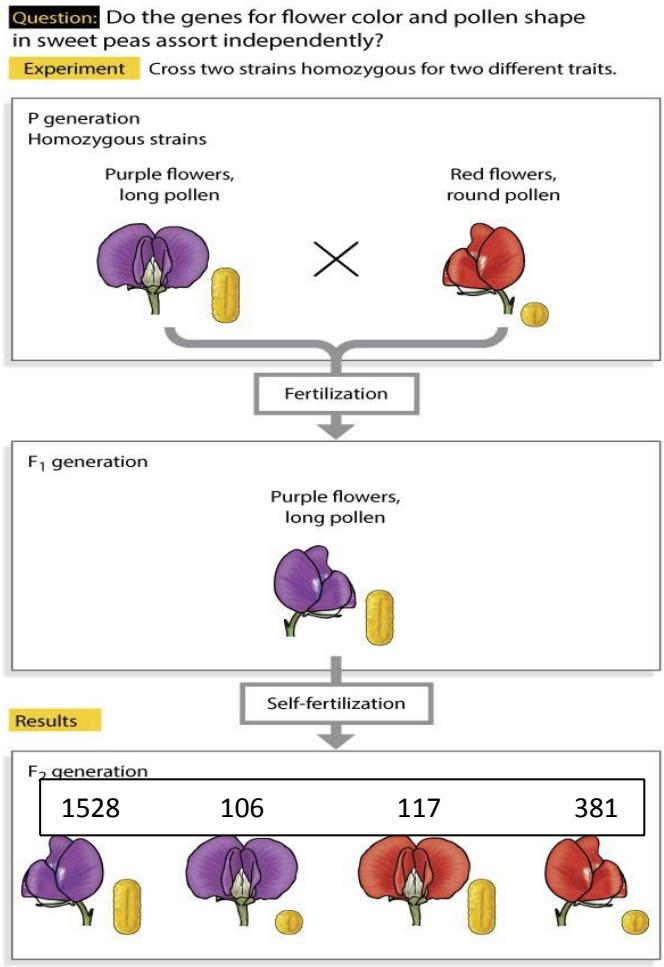


Figure (1st trial)

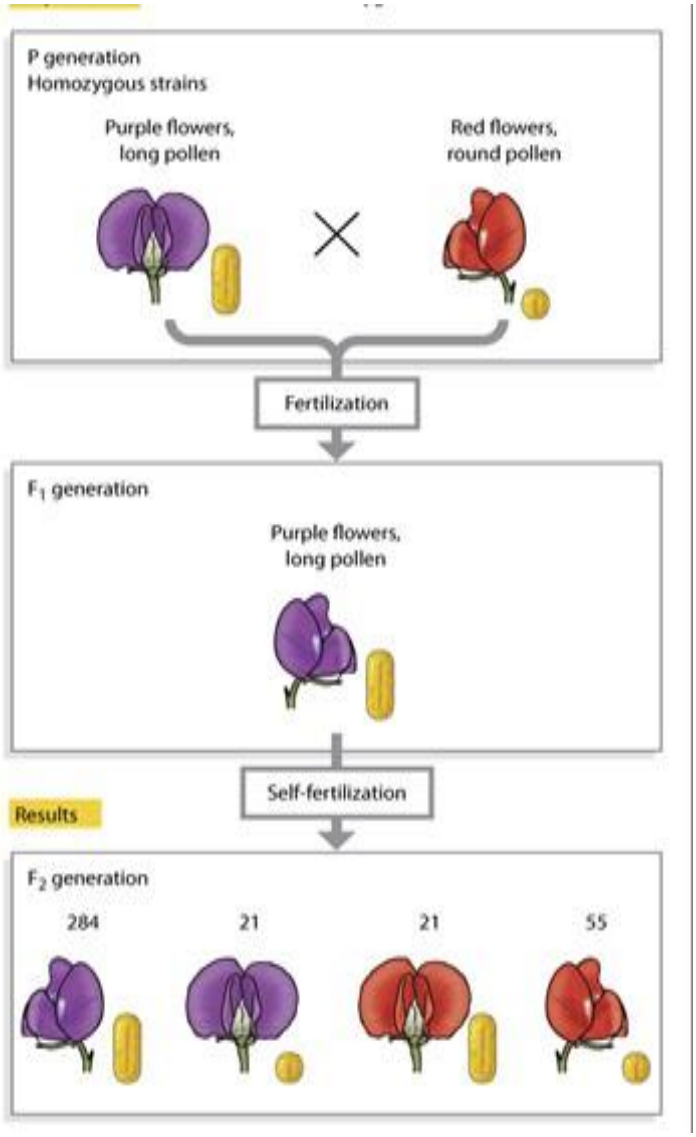
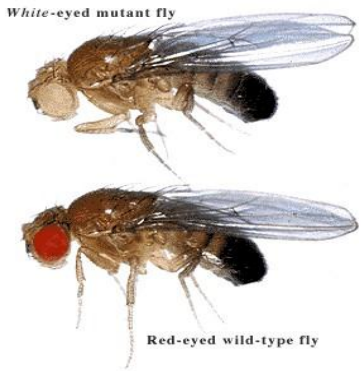


Figure (other trial)

But why are certain alleles linked? Bateson, Saunders, and Punnett weren't sure. In fact, the answer to this question came just seven years later (1912), when Thomas Hunt Morgan used fruit flies to demonstrate that linked genes must be real physical objects that are located in close proximity on the same chromosome.

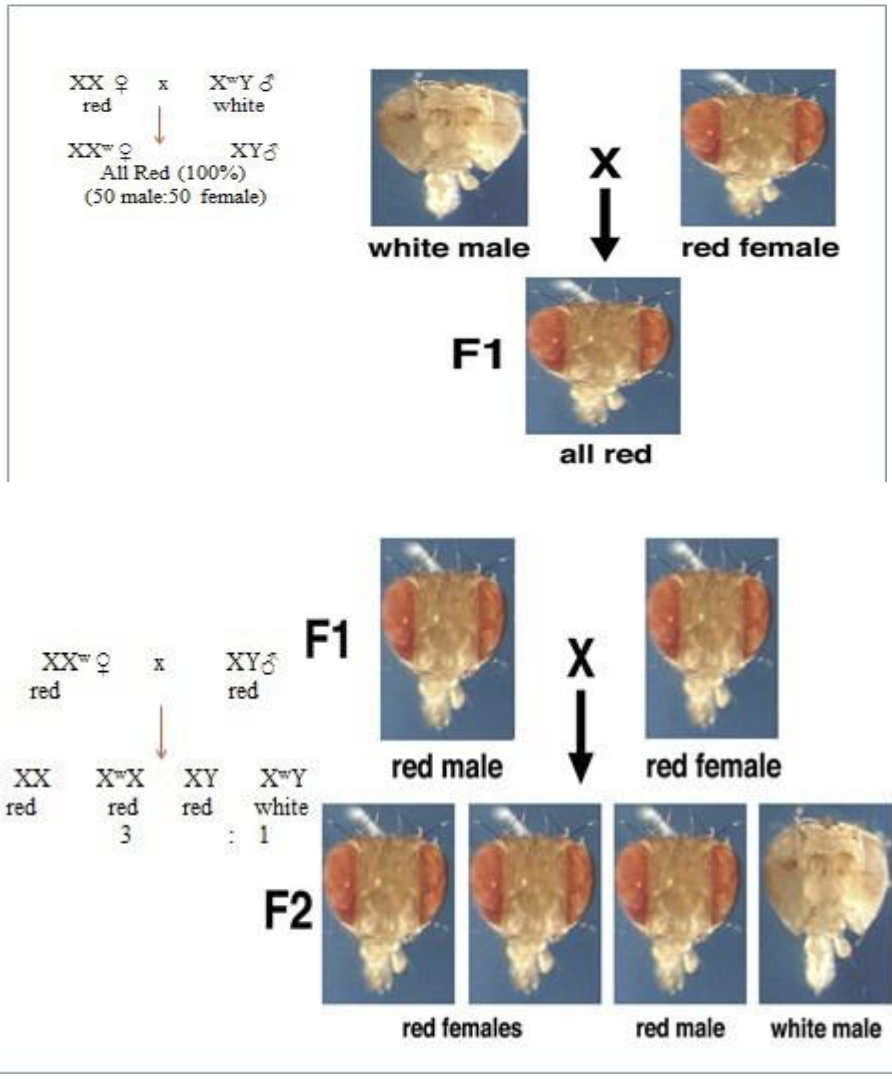
Morgan Finds Answers in the White-Eyed Fly

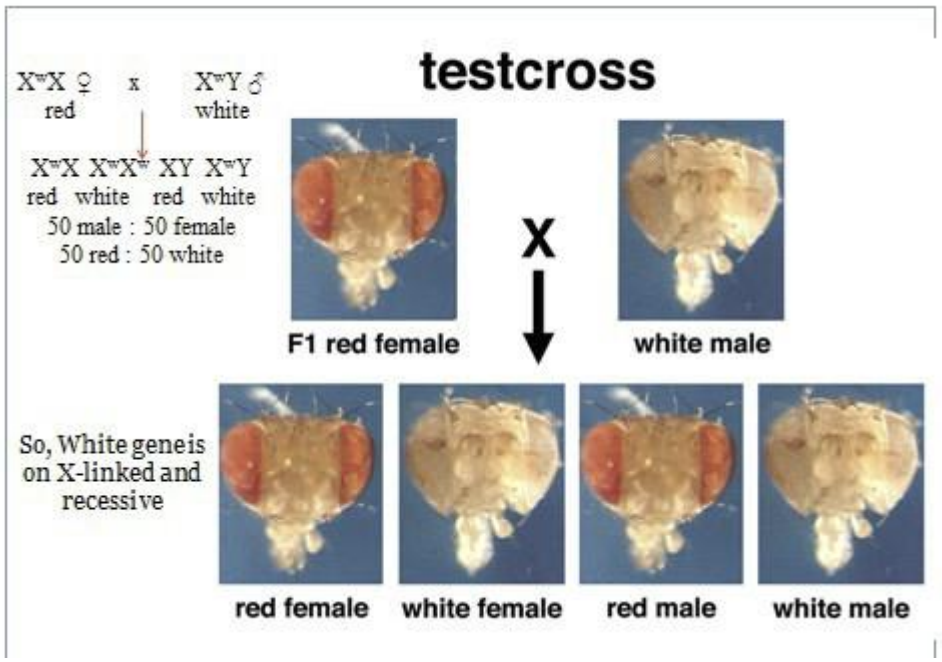
At the beginning of the 20th century, Thomas Hunt Morgan's famous "fly room" at Columbia University was the site of many discoveries and **"eureka"** moments in the field of genetics. Morgan chose to use the prolific fruit fly *Drosophila melanogaster* as a model to study genetics. Then, for a period of three years, Morgan and his students struggled to find a way to create a fly that looked different from normal flies (Normal fruit flies have red eyes) by treating these flies with heat, cold, X-rays, acids, bases, sugars, and other chemicals.



In 1910, Morgan fortuitously discovered a single fly with white eyes that did not result from any of his treatments (Normal fruit flies have red eyes, not white eyes). Morgan immediately crossed this white-eyed male fly to its red-eyed sisters. Interestingly, when Morgan later inbred (cross) the heterozygous F_1 red-eyed flies, the traits of the F_2 progeny did not assort independently. Morgan expected a 1:1:1:1 ratio of red-eyed females, red-eyed males, white-eyed males, and white-eyed females. Instead, he observed the following phenotypes in his F_2 generation: 2,459 red-eyed females, 1,011 red-eyed males and 782 white-eyed males (figure below). There were no white-eyed females, and Morgan wondered whether this was because the trait was sex-limited and only expressed in male flies. To test whether this was indeed the case, Morgan performed a

test cross between the original white-eyed male fly and some of his F_1 daughters (red-eyed). These crosses produced a generation with the following phenotypes: 129 red-eyed females, 132 red-eyed males, 88 **white-eyed females** and 86 white-eyed males (figure below). Thus, the results of this cross did produce white-eyed females, and the groups had approximately equal numbers. Morgan therefore hypothesized that the eye-color trait was connected with the sex factor (X-linked gene). This in turn led to the idea of genetic linkage, which means that when two genes are closely associated on the same chromosome, they do not assort independently.





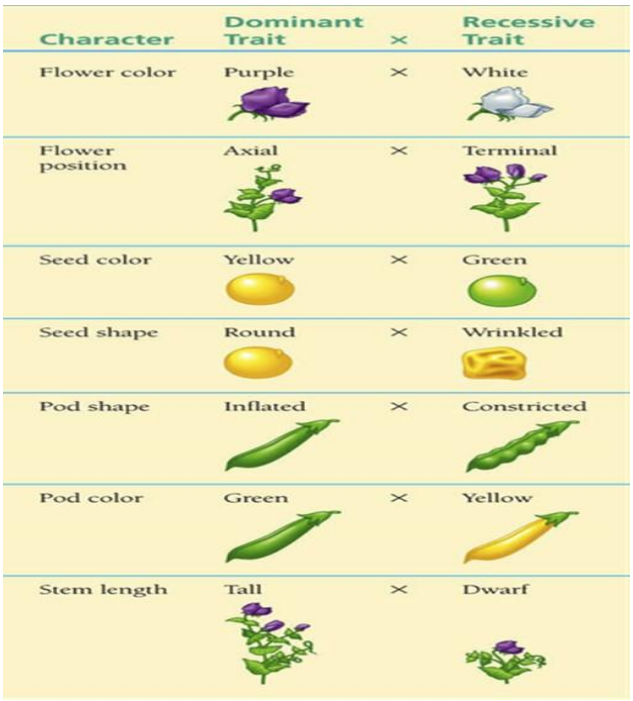
Morgan's proposal was an early suggestion that genes were real, physical objects that were located on chromosomes. Indeed, knowledge of genetic linkage was critical to prove that genes were actual objects that could be inherited, undergo recombination, and be mapped to specific locations on chromosomes.

For instance, after Morgan's findings were published, Reginald C. Punnett (1923-1927) used this information to identify linkage groups in his previous plant studies, and he associated these linkage groups with chromosomes. Also, with this knowledge in place, Morgan and Alfred H. Sturtevant, his student, conducted further studies of linkage that provided information regarding gene location on chromosomes and ultimately resulted in gene mapping.

Why Didn't Mendel Observe Linkage?

So if linkage exists, why didn't Mendel detect it while carrying out his crosses in pea plants?

-In part, this was the case because Mendel studied seven traits of seven genes (monogenic traits), and the pea plant has seven chromosomes.



Character	Dominant Trait	×	Recessive Trait
Flower color	Purple	×	White
Flower position	Axial	×	Terminal
Seed color	Yellow	×	Green
Seed shape	Round	×	Wrinkled
Pod shape	Inflated	×	Constricted
Pod color	Green	×	Yellow
Stem length	Tall	×	Dwarf

Still, Mendel didn't choose pairs of genes that were always on different chromosomes; some of the pairs of genes that Mendel studied were actually on the same chromosomes, as shown in Table 2 (below).

Relationship between modern genetic terminology and character pairs used by Mendel

Character pair used by Mendel	Alleles in modern terminology	Located in chromosome
Seed colour, yellow–green	*I–i*	1
Seed coat and flowers, coloured–white	*A–a*	1
Mature pods, smooth expanded–wrinkled indented	*V–v*	4
Inflorescences, from leaf axils–umbellate in top of plant	*Fa–fa*	4
Plant height, >1m–around 0.5 m	*Le–le*	4
Unripe pods, green–yellow	*Gp–gp*	5
Mature seeds, smooth–wrinkled	*R–r*	7

-Since the publication of Mendel's findings, other scientists have performed the pea plant crosses that could have shown linkage: *i-a*, *v-fa*, *v-le*, and *fa-le*. However, all of the pairs, except *v-le*, are so distantly (far) located that Mendel would have been unable to detect linkage. In other words, although these pairs of genes are syntenic, they are not statistically linked so, they behave as they independently assort. The *v-le* cross, on the other hand, would have shown linkage if Mendel had completed the cross. Possibly, with just one more cross, Mendel would have discovered linkage himself.

Thomas Hunt Morgan, Genetic Recombination, and Gene Mapping

In 1911, while studying the chromosome theory of heredity, biologist Thomas Hunt Morgan had a major breakthrough. Morgan occasionally noticed that "linked" traits would separate. Meanwhile, other traits on the same chromosome showed little detectable linkage. Morgan

considered the evidence and proposed that a process of crossing over, or recombination, might explain his results. Specifically, he proposed that the two paired chromosomes could "crossover" to exchange information.

Today, we know that recombination does indeed occur during prophase of meiosis (Figure below), and it creates different combinations of alleles in the gametes that result (i.e., the F_1 generation; Figure below).

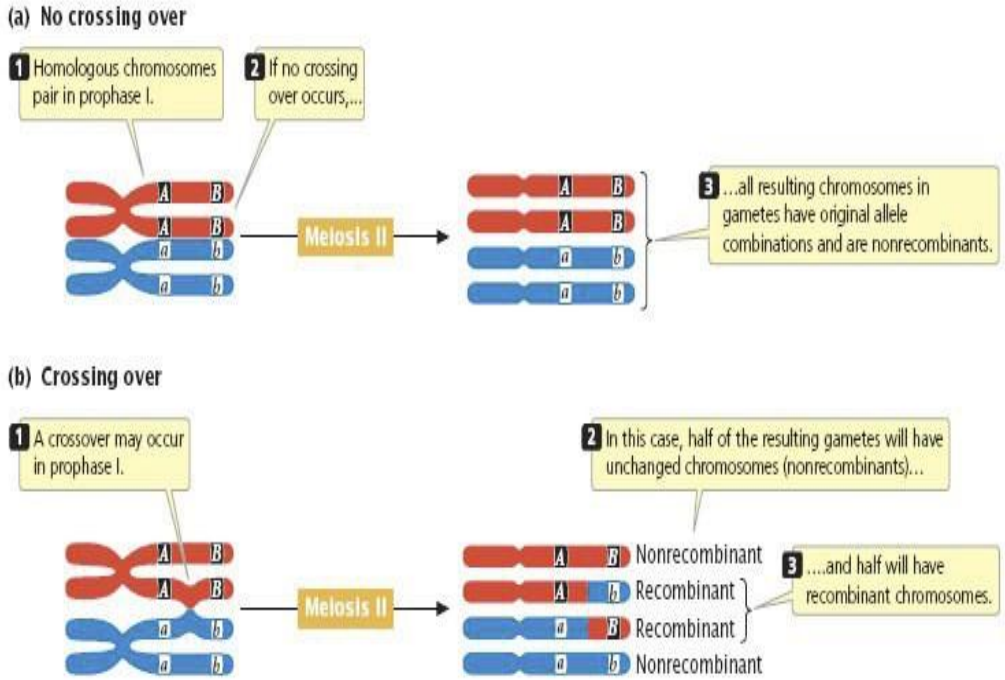


Figure 3

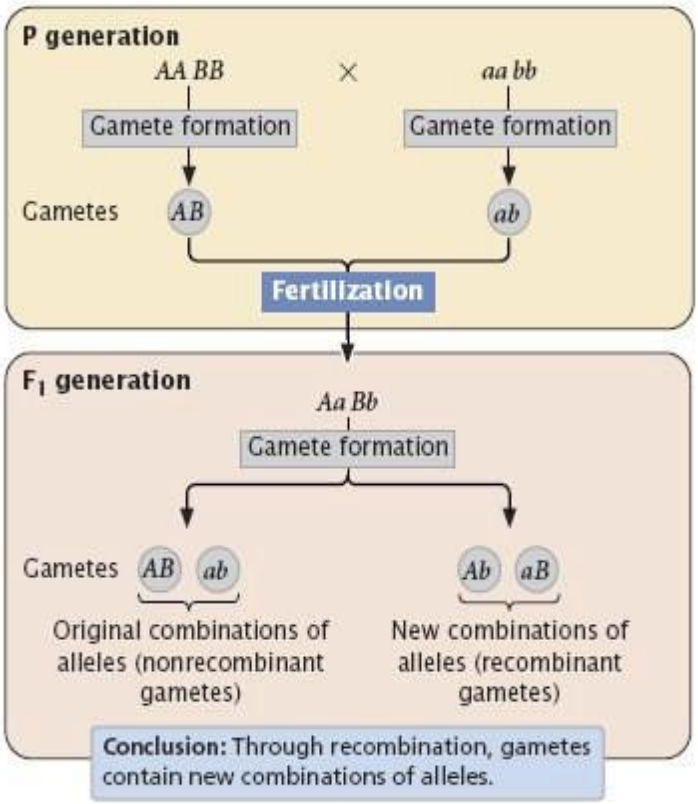
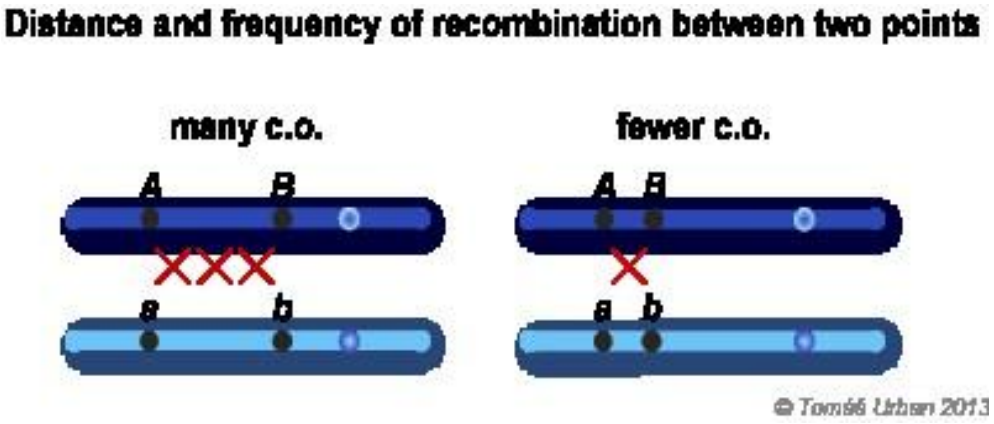


Figure 4

When proposing the idea of crossing over, Morgan also hypothesized that the frequency of recombination was related to the distance between the genes on a chromosome, and that the interchange of genetic information broke the linkage between genes. Morgan imagined that genes on chromosomes were similar to pearls on a string i.e. they were physical objects. The closer two genes were to one another on a chromosome, the greater their chance of being inherited together. In contrast, genes located farther away from one another on the same chromosome were more likely to be separated during recombination. Therefore, Morgan correctly proposed that the strength of linkage between two genes (or their frequency of recombination) depends upon the distance between the genes on the chromosome, figure below. This

proposition became the basis for construction of the earliest maps of the human genome.



Sturtevant Uses Crossing-Over Data to Construct the First Genetic Map

Soon after Morgan presented his hypothesis, Alfred Henry Sturtevant, a 19-year-old Columbia University undergraduate who was working with Morgan, realized that if the frequency of crossing over was related to distance, one could use this information to map out the genes on a chromosome. After all, the farther apart two genes were on a chromosome, the more likely it was that these genes would separate during recombination. Therefore, as Sturtevant explained it, the "proportion of crossovers could be used as an index of the distance between any two factors". Collecting a stack of laboratory data, Sturtevant went home and spent most of the night drawing the first chromosomal linkage map for the genes located on the X chromosome of fruit flies.

When creating his map, Sturtevant started by placing six X-linked genes in order. B was a gene for black body color. C was a gene that allowed color to appear in the eyes. Flies with the P gene had vermilion eyes instead of the ordinary red, and flies with two copies of the recessive O gene had eyes that appeared a shade known as eosin. The R and M

factors both affected the wings. Sturtevant placed C and O at the same point because they were completely linked and were always inherited together — in other words, he never saw any evidence for recombination between C and O. Sturtevant then placed the remainder of the genes in the order shown in Figure below. Crossover events were tracked by examining the F_2 progeny in crosses for "new" phenotypes.

In addition to describing the order of the genes on the X chromosome of fruit flies, Sturtevant's 1913 paper elucidated a number of other interesting points, including the following:

- The relationship between crossing over and genetic map distance
- The effects of multiple crossover events
- The fact that a first crossover can inhibit a second crossover (a phenomenon called interference)

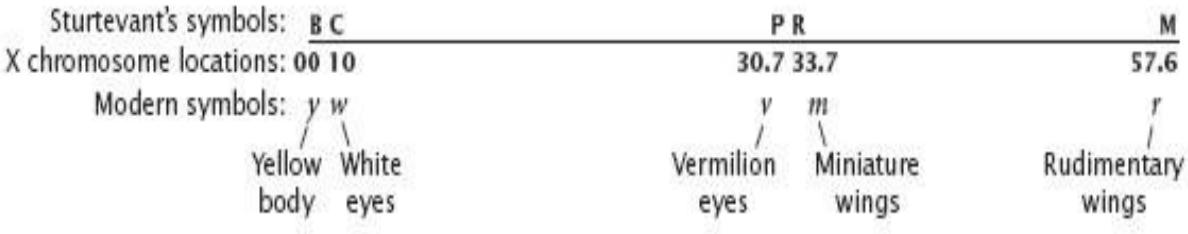


Figure : Sturtevant's map included five genes on the X chromosome of Drosophila. The genes are yellow body (y), white eyes (w), vermilion eyes (v), miniature wings (m), and rudimentary wings (r). Sturtevant's original symbols for the genes are shown above the line; modern symbols are shown below with their current locations on the X chromosome. *Note that the O gene was shown to be completely linked to C.

Rules of Mapping Genes Using Recombination Frequency

Sturtevant then worked out the order and the linear distances between these linked genes, thus forming a linkage map. In doing so, he computed the distance in an arbitrary unit he called the **"map unit,"**

which represented a recombination frequency of 0.01, or 1%. Later, the map unit was renamed the centimorgan (cM), in honor of Thomas Hunt Morgan, and it is still used today as the unit of measurement of distances along chromosomes.

In order to calculate the recombination frequency we use the following formula:

$$\text{Recombination frequency (\%)} = \frac{\text{\# Recombinant progeny}}{\text{Total\# progeny}} \times 100$$

The percentage of recombinants ranges from 1 to 50% with gene loci on separate chromosomes (independent assortment). But this equivalence is only a good approximation for small percentages; the largest percentage of recombinants cannot exceed 50%, which would be the situation where the two genes are at the extreme opposite ends of the same chromosomes.

1% recombinants = 1 cM

The higher the percentage of recombinants for a pair of traits, the greater the distance separating the two loci.

NOTE:

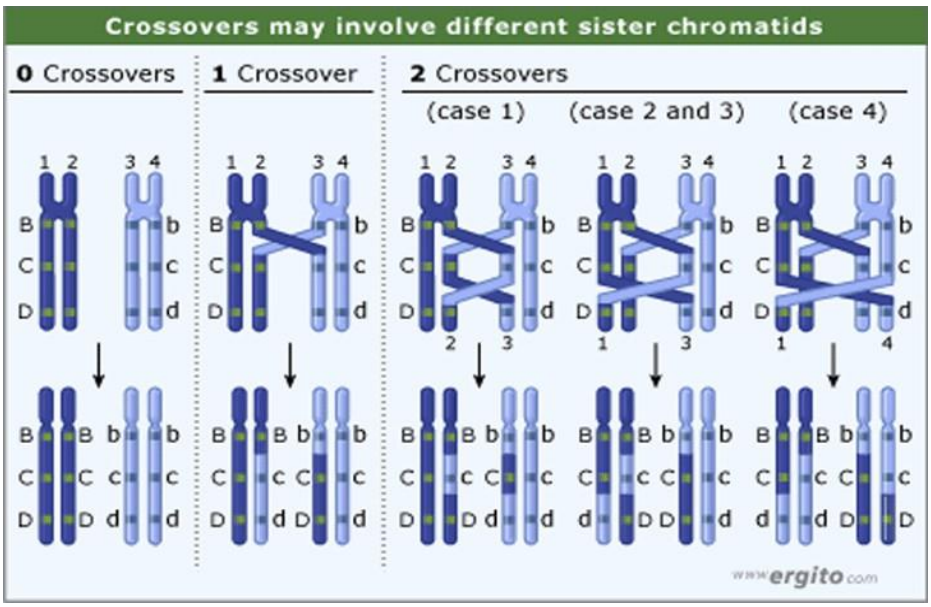
- A map unit is also equivalent to the physical distance along a chromosome which will experience 1 crossover event in every 50 meiotic divisions (1 crossover in 50 meiotic divisions = 2 recombinant gametes in every 200 = 1 % recombination). So, two genes that recombine with a frequency of 1% are said to be 1 mapunit apart.
- **Number of recombinants depend on number of reproductive cells perform crossover:** If We Have 100 Reproductive Cells: 80 cells

will not perform cross over, they will produce 320 parental gametes. The other 20 cells will perform crossover producing 80 gametes (40 parental and 40 recombinant). The parental gametes will be 90% while, the recombination frequency will be 10%.

There are other problems with preparing genetic maps of chromosomes:

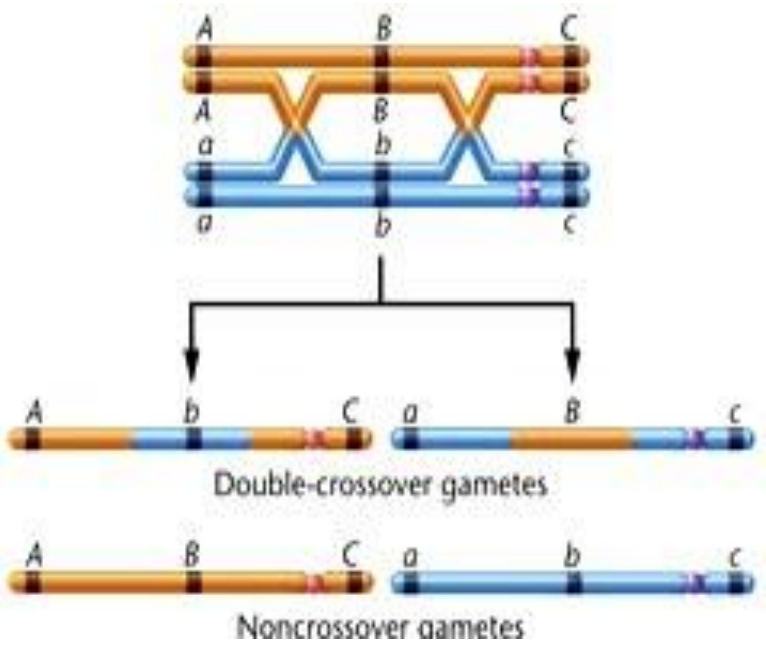
- The probability of a crossover is not uniform along the entire length of the chromosome.
- Crossover is inhibited in some regions (e.g., near the centromere).
- Some regions (especially at edges) are "hot spots" for recombination (for reasons that are not clear). Approximately 80% of genetic recombination in humans is confined to just one-quarter of our genome.
- In humans, the frequency of recombination of loci on most chromosomes is higher in females than in males. Therefore, genetic maps of female chromosomes are longer than those for males.

Different forms of crossover:



Three-point crosses can be used to put genes in order

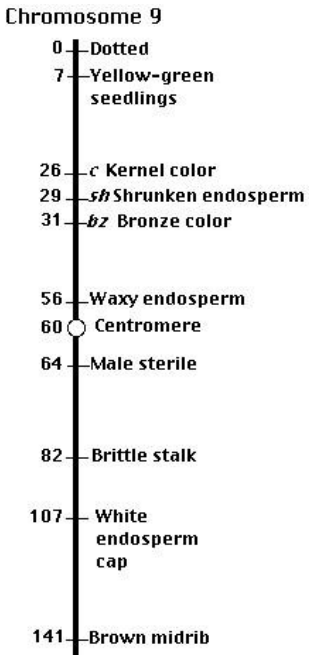
Because multiple crosses reduce the number of observed recombinant progeny, longer map distances are not acute. As a result, when geneticists try to construct maps from a series of two-point crosses, determining the order of genes is problematic. Using three loci instead of two, or a three-point cross, can help solve the problem. In a three-point cross, the gene in the middle allows us to see recombination events on either side. A double crossover for the two outside loci is actually a single crossover between each outside locus and the middle locus. The probability of two crossovers is equal to the product of the probability of each individual crossover, each of which is relatively low (table below). Therefore, in any three-point cross, the offspring with two crossovers is the least frequent data. Analyzing these individuals to see which locus is recombinant identifies the locus that lies in the middle of the three loci in the cross (figure below).



Figure

Examples of Mapping Genes

A genetic map of chromosome 9 (the one that carries the C, Sh, and bz loci) of the corn plant (*Zea mays*) is shown below (figure below). If one maps in small intervals from one end of a chromosome to the other, the total number of centimorgans often exceeds 100 (as you can see for chromosome 9). However, even for widely-separated loci, the maximum frequency of recombinants that can form is 50% and this is also the frequency of recombinants that we see for genes independently assorting on separate chromosomes. So we cannot tell by simply counting recombinants whether a pair of gene loci is located far apart on the same chromosome or are on different chromosomes.



Start with two different strains of corn (maize). One that is homozygous for yellow kernels (C,C) smooth (Sh,Sh) and a second that is homozygous for colorless kernels (c,c) shrunken (sh,sh). When the pollen of the first strain is dusted on the silks of the second (or *vice versa*), the

kernels produced (F_1) are all yellow and smooth (CcShsh). So, the alleles for yellow color (C) and smoothness (Sh) are dominant over those for colorlessness (c) and shrunken endosperm (sh).

To simplify the analysis, mate the dihybrid with a homozygous recessive strain (ccshsh). Such a mating is called a test cross because it exposes the genotype of all the gametes of the strain being evaluated (table below).

Genotype of all gametes formed by c,c,sh,sh parent	Genotypes of gametes formed by heterozygous (C,c,Sh,sh) parent			
	CSh	csh	Csh	cSh
csh	Genotypes of offspring: C,c,Sh,sh	c,c,sh,sh	C,c,sh,sh	c,c,Sh,sh
Appearance (phenotype)	Colored, smooth	Colorless, wrinkled	Colored, wrinkled	Colorless, smooth
If independent assortment	25%	25%	25%	25%
Actual results	48.5%	48.5%	1.5%	1.5%

According to Mendel's second rule, the genes determining color of the endosperm should be inherited independently of the genes determining texture. The F_1 should thus produce gametes in approximately equal numbers.

- CSh, as inherited from one parent.
- csh, as inherited from the other parent ·

Csh, a recombinant

- cSh, the other recombinant.

All the gametes produced by the doubly homozygous recessives would be csh.

If the inheritance of these genes observes Mendel's second rule; i.e., shows independent assortment, union of these gametes should produce approximately equal numbers of the four phenotypes (25%). But as the chart shows, there is instead a strong tendency for the parental alleles to stay together (97%). It occurs because the two loci are relatively close together on the same chromosome. Only 3.0% of the gametes contain a recombinant chromosome, so the c and sh loci are said to be 3.0 cM apart.

During prophase I of meiosis, pairs of duplicated homologous chromosomes unite in synapsis and then non-sister chromatids exchange segments during crossing over. It is crossing over that produces the recombinant gametes. In this case, whenever a crossover occurs between the locus for kernel color and that for kernel texture, the original combination of alleles (CSh and csh) is broken up and a chromosome containing Csh and one containing cSh will be produced.

Test crossing a corn plant that is dihybrid for the C,c alleles and the alleles for bronze color (Bz, bz) produces 4.6% recombinants. So these two loci are 4.6 cM apart. However, is the bz locus on the same side of c as sh or is it on the other side?

The answer can be found by test crossing the dihybrid Shsh, Bzbz. If the percentage of recombinants is less than 4.6%, then bz must be on the same side of locus c as locus sh. If greater than 4.6%, it must be on the other side. In fact, the recombination frequency is 2.0%, telling us that the actual order of loci is (figure 7): c — sh — bz.

Mapping by linkage analysis is best done with loci that are relatively close together; that is, within a few centimorgans of each other. Why? Because as the distance between two loci increases, the probability of a second crossover occurring between them also increases.

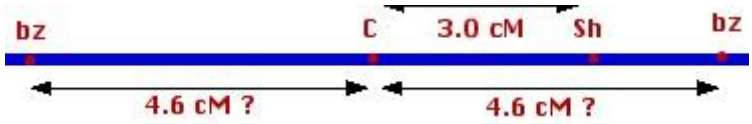
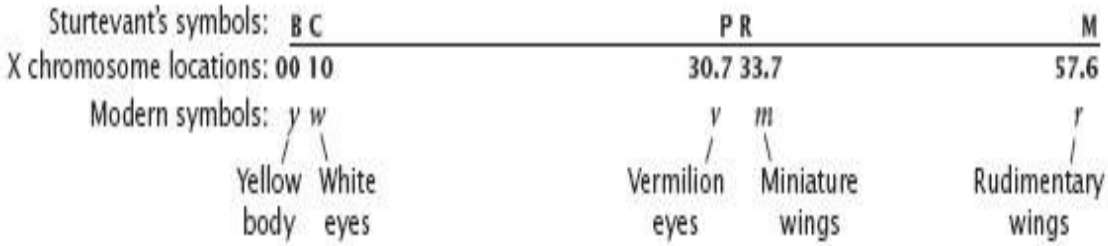


Figure 7

Deviations from Expected Results Revealed Genetic Interference

Sturtevant also described the fact that, for genes that were distant from one another, there was a discrepancy in the predicted number of crossovers. For example, the distance between B and M on his map (figure below) was 57.6. His recombination data using those two genes, however, did not suggest this distance. Instead, Sturtevant found 260 recombinants in 693 male progeny, which, when plugged into the equation, produced a result of 37.6.



How, then, did Sturtevant explain the deviation? Sturtevant realized that double recombination events could occur if genes were far apart. Moreover, not only did Sturtevant's data suggest that double-crossover occurred, but it also suggested that an initial crossover event could inhibit subsequent events by way of a phenomenon Sturtevant referred to as **interference**.

The detection of the double recombinant classes shows that double crossovers must occur. Knowing this, we can ask, are the crossovers in

adjacent chromosome regions independent or does a crossover in one region affect the likelihood of there being a crossover in an adjacent region. It turns out that often they are not independent showing interference.

If this deficiency of double recombinants were consistently observed, it would show us that the two regions are not independent and suggest that the distribution of crossovers favors singles at the expense of doubles. In other words, there is some kind of interference*:* the tendency (how strong) crossover between two pairs of genes to reduce the probability of a crossover of one of those genes with a different gene in an adjacent region.

How can we detect interference?

Second crossover would undo the effect of the first crossover and restore the parental combination of alleles. These would show up as non-recombinants. Thus, as the distance between two loci increases, the percentage of recombinants that forms understates (less than) the actual (expected) distance in centimorgans that separates them.

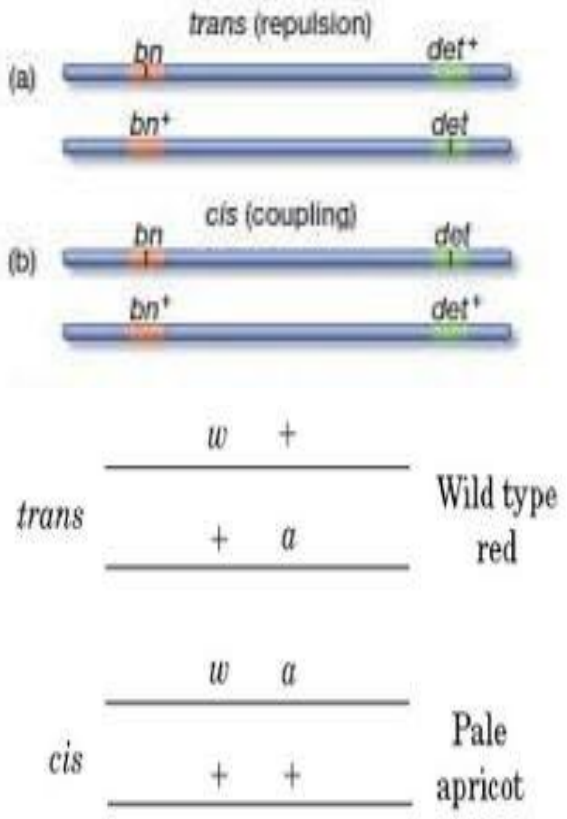
GENETIC TERMS

Complete and Incomplete Linkage

When Sturtevant drew his chromosomal map, he placed the C and O genes at the same location because they were always inherited together (figure 5). Genes that are so close together on a chromosome that they are always inherited as a single unit show a relationship referred to as **complete linkage**. Those completely linked genes can only be differentiated as separate genes when a mutation occurs in one of them. There is no other way to identify genes with complete linkage from single genes that show multiple phenotypes.

On the other hand, the phenomenon known as **incomplete linkage** occurs when two genes show linkage with a recombination level ≤ 50% i.e. all expected types of gametes are formed, but the recombinant gametes occur less often than the parental gametes. In addition, if two genes are on the same chromosome and are far enough apart that they undergo recombination at least 50% of the time, the genes are independently assorting and do not show linkage at a distance of 50 cM or more apart (>50 cM). This means that in this case no statistical test would allow researchers to measure linkage. Finally, linked genes that do not independently assort show statistical linkage as deviation from independent assortment that favors the parental gametes (i.e. parental gametes are greater than recombinant ones).

When the progeny received two dominant alleles linked on one chromosome (bn^+ det^+) and its homologous has both recessive alleles (bn det), so the alleles will be in **Cis (coupling) arrangement.** On the other hand, when the progeny received one parental chromosome with a dominant allele for one trait (bn^+) linked to a recessive allele for a second trait (det), *vice versa* for the other parental chromosome (bn det^+), so alleles will be in **Trans (repulsion) arrangement** (figure)**.**



Figure

For more readings:

1. Essentials of Genetics, 8th edition, Klug, Cummings, Spencer, Palladino (eds.), 2013 (online).
2. Biology, 8th edition, 2008, Losos, Mason and Singer (eds.) (in Botany Department Library).
3. Genomes, 2nd edition, 2002, Brown (ed.). (online)

Animations:

Meiosis with crossover:

http://highered.mcgraw-hill.com/sites/dl/free/0072835125/126997/animation5.html

Linked genes:

http://www.dnatube.com/video/27686/Explanation-of-Linked-Genes